EMBRYOLOGY OF DRIMYS WINTERI

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Drimys is one of six genera of the vesselless family, Winteraceae. The genus includes nearly 40 species of which 36 occur in the Old World and the rest are found in the Americas. The family is of interest because of the presence of numerous primitive characters such as the undifferentiated stamens in some members; a complete series from an open conduplicate to a closed carpel which may be sessile or stipitate; stigmatic crest; laminar placentation, and primitive xylem without vessels.

Bailey (1944), Bailey and Nast (1943a, b; 1944a, b; 1945), and Nast (1944) have dealt extensively with the morphology and vegetative anatomy of various members of the Winteraceae. However, literature on its embryology is rather meager. Maheshwari (1950), while discussing the relationships of angiosperms with other groups, has remarked "Regarding the relationship of the angiosperms with other groups, we are at present entirely in the dark. It is possible that a study of morphology and embryology of Degeneriaceae, Winteraceae, Trochodendraceae etc., may throw some light on the problem." So a study of the embryology of the Winteraceae was taken up (see Bhandari, 1963) and the present investigation is a continuation of that project.

PREVIOUS WORK

Strasburger (1905) made some preliminary observations on the ovule and embryo sac of *Drimys winteri* var. *winteri* and reported normal embryo sac and nuclear endosperm. Bhagawathi Kutti Amma (1938) studied the details of microsporogenesis in *Drimys* and recorded amoeboid anther tapetum. On the other hand, Swamy (1952) observed secretory tapetum, normal embryo sac, and cellular endosperm in *Zygogynum baillonii*. In *Pseudowintera colorata* (Bhandari, 1963) the tapetum is amoeboid but in *P. axillaris* (Sampson, 1963) it is secretory. In both species the embryo sac is of the Polygonum type, and endosperm is cellular. Post-fertilization stages in the ovules and pericarp have been followed only in *P. colorata* (Bhandari, 1963).

MATERIAL AND METHODS

The buds, flowers, and fruits of *Drimys winteri* were obtained by the late Professor P. Maheshwari through the courtesy of Dr. V. Garcia of Argentina. The collections were fixed on the spot in FAA and later stored in 70 percent ethanol. The material was passed through alcohol-

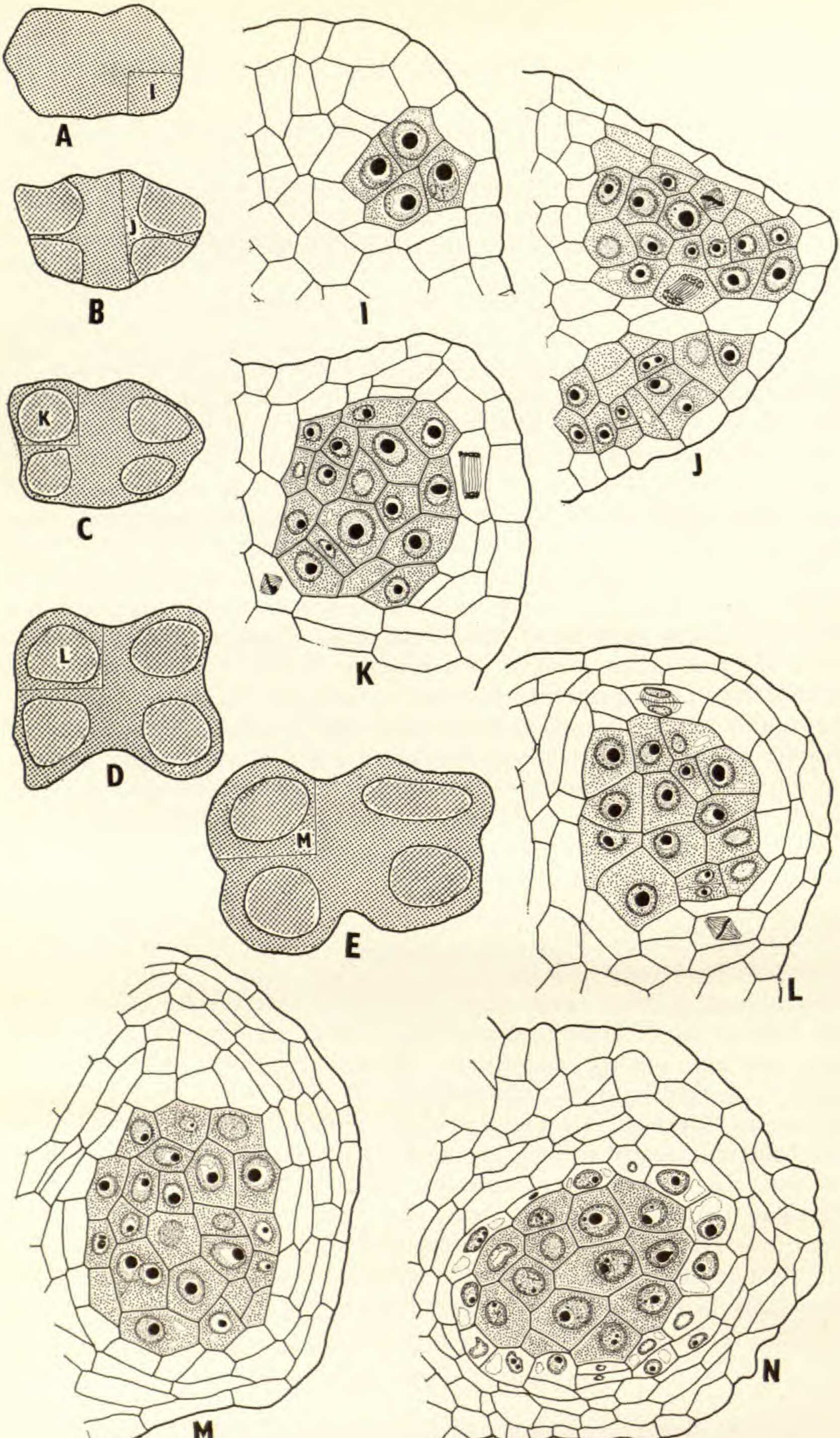
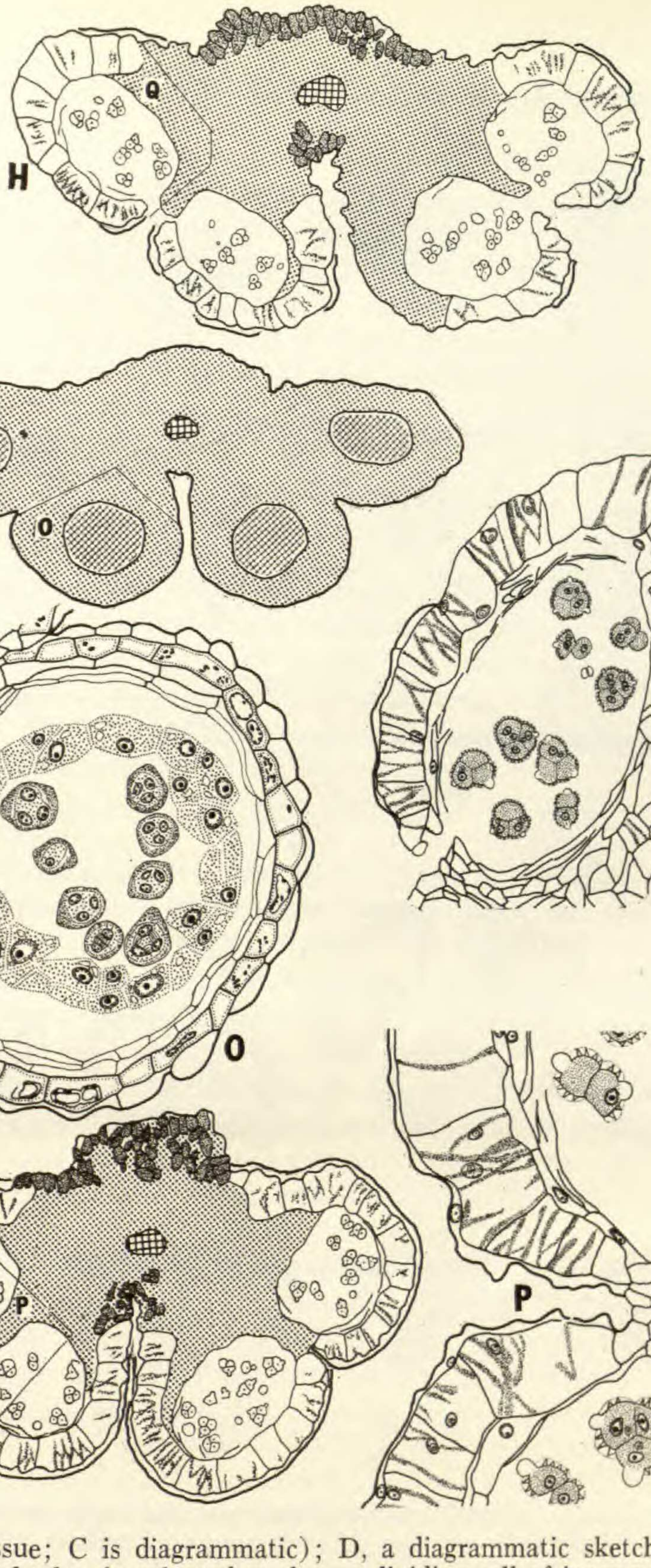


FIG. 1. *Drimys winteri*, microsporangium. A, I, transection of anther showing archesporium; B, J, transection of anther (J is an enlargement of a portion of B showing some archesporial cells in division, sporogenous tissues, and a parietal layer); C, K, cross section of anther at the stage of organization of wall layers (wall comprises an epidermis, two parietal layers, and central



sporogenous tissue; C is diagrammatic); D, a diagrammatic sketch for L; L, representation of a locule enlarged to show a dividing cell of inner parietal layer which contributes to the tapetum and middle layer II; E, M, transection of anther, one locule showing the epidermis, endothecium, 2 middle layers, tapetum, and the sporogenous tissue; N, *the same*, note that the tapetum is well developed; F, O, cross sections of anther, O is a portion enlarged to show numerous microspore mother cells, surrounding them during meiosis is the detached tapetum; G, P, *the same*, showing pollen grains, the septum is intact in P; H, Q, transection of dehisced anther, the portion marked Q in H is enlarged, note that at time of dehiscence mainly the endothecial layer persists while the others degenerate. A–E, all × 165; F–H, all × 80; I–K, all × 640; L, × 540; M, × 540; N, × 300; O, × 300; P, × 220; Q, × 125.

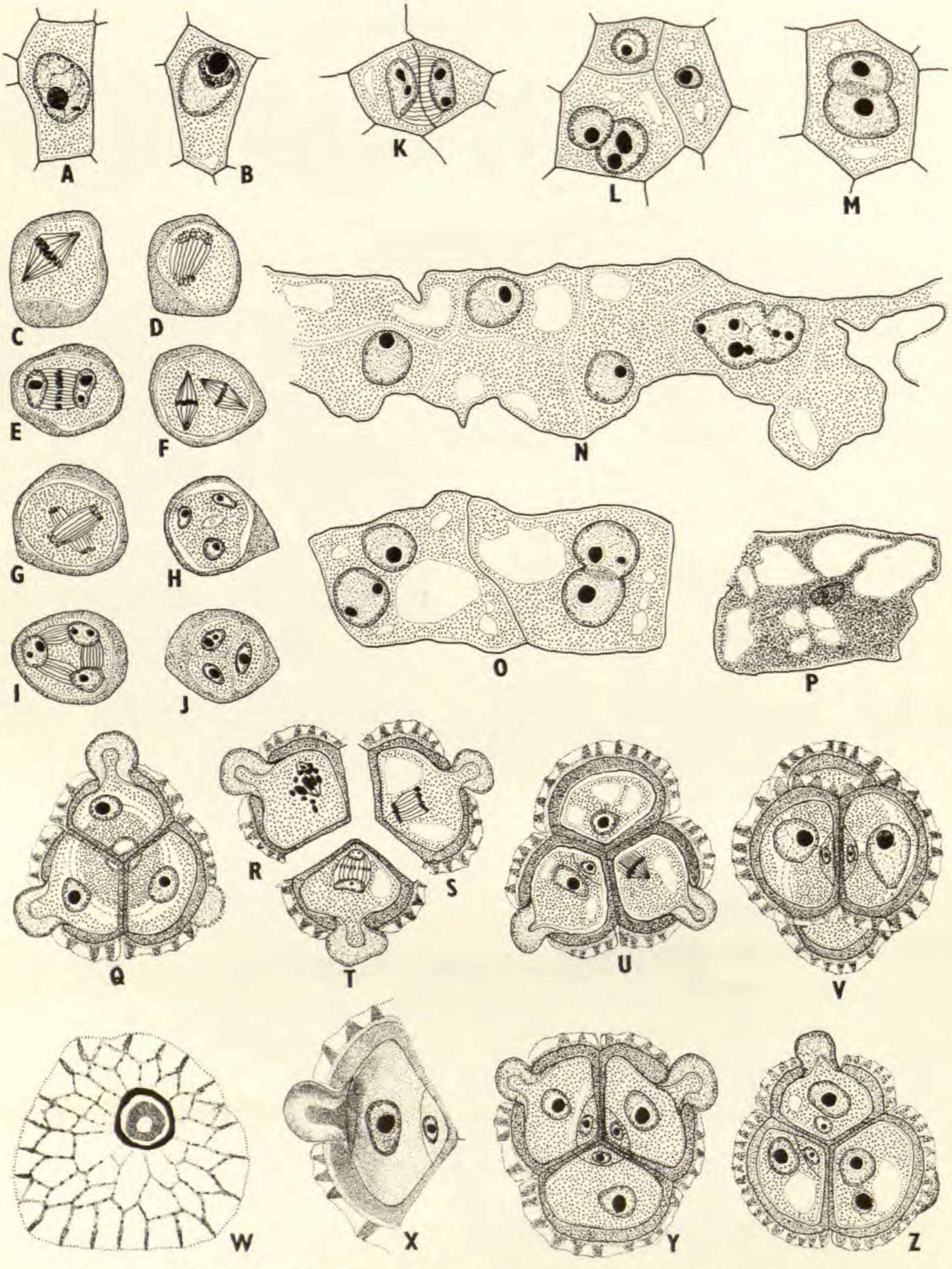


FIG. 2. *Drimys winteri*, microsporogenesis and male gametophyte. A–J, microspore mother cells showing different stages of meiosis, note that an incipient cell plate is formed after Telophase I in E; K–O, stages in the formation of occasionally bilayered tapetum with binucleate cells, the nuclei fuse to form polyploid masses in M and N; P, a degenerating tapetal cell; Q, a tetrahedral tetrad showing microspores with exine and intine, the intine much thickened at the region of germ pore through which it protrudes; R–T, three microspores showing different stages of division in the formation of the generative cell towards the proximal pole; U, single tetrad showing three microspores at different stages of division; V, a decussate tetrad with 2-celled pollen grains; W, polar view of a pollen grain showing the pattern of the exine, germ

xylene series and later embedded in paraffin. The seeds (mature seeds without seed coat) were run through the above or through the tertiary butyl alcohol series. Prior to sectioning, the embedded material (especially the seeds) was soaked in water or in 30 percent glycerine at room temperature for two weeks to facilitate microtomy. The sections were cut 6 to 14 microns thick and the preparations were stained with safranin-fast green, but those of seed development stained better with hematoxylin-eosin combination. Hand sections of mature seeds mounted in 15 percent glycerine were also examined to study the seed structure.

OBSERVATIONS

Microsporangium. The young anther is histologically undifferentiated with a well defined epidermis enclosing a homogeneous mass of cells. As the anther enlarges, in each of the four corners, a group of four or five hypodermal archesporial cells differentiates (FIGS. 1A, I). The hypodermal cells divide periclinally to form the primary parietal layer and the sporogenous layer, while the subhypodermal ones directly form the sporogenous tissue (FIGS. 1B, J). They divide mitotically to add to the sporogenous tissue (FIG. 1J). The primary parietal layer undergoes a periclinal division to form two layers (FIGS. 1C, D, K, L). The outer forms the endothecium and middle layer I, while the inner gives rise to the tapetum and middle layer II (FIGS. 1E, M, N).

The epidermal cells become tangentially compressed and highly vacuolated; their nuclei start degenerating but they stay as a thin layer of collapsed cells at the time of anther dehiscence (FIGS. 1G, H, P, Q). During meiosis, the endothecial cells enlarge radially, develop strong fibrous thickenings (FIGS. 1F–H, O–Q), and are persistent in the mature anther (FIGS. 1H, Q). A few cells of the connective also develop such thickenings (FIG. 1Q). The middle layers remain healthy until the beginning of meiosis but soon after their cells become flattened. Consequently, the tapetum becomes detached and lies as an isolated layer inside the anther locule, surrounding the dividing microspore mother cells (FIGS. 1F, O). The tapetal cells show high metabolic activity, become binucleate (FIGS. 2K, L) and their nuclei fuse and form large polyploid masses (FIGS. 2M–O). Soon the walls separating the adjacent tapetal cells become dissolved (FIGS. 1O, 2N), and after the formation of microspore tetrads, the cells show signs of degeneration *in situ* (FIG. 2P). At a time when the exine is differentiating the tapetum gets absorbed completely.

Microsporogenesis and Male Gametophyte. Meiosis of microspore mother cells is non-synchronous. During heterotypic division (FIGS. 2A–

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pore, and the dumbbell-shaped protrusion of intine; X, one microspore enlarged to show the protruding intine and the collar formed at the base of the protrusion due to thickening of the intine; Y, two-celled pollen grains in a tetrahedral tetrad; Z, pollen tetrad at the shedding stage. A–V, all × 780; W, X, both × 935; Y and Z, × 780.

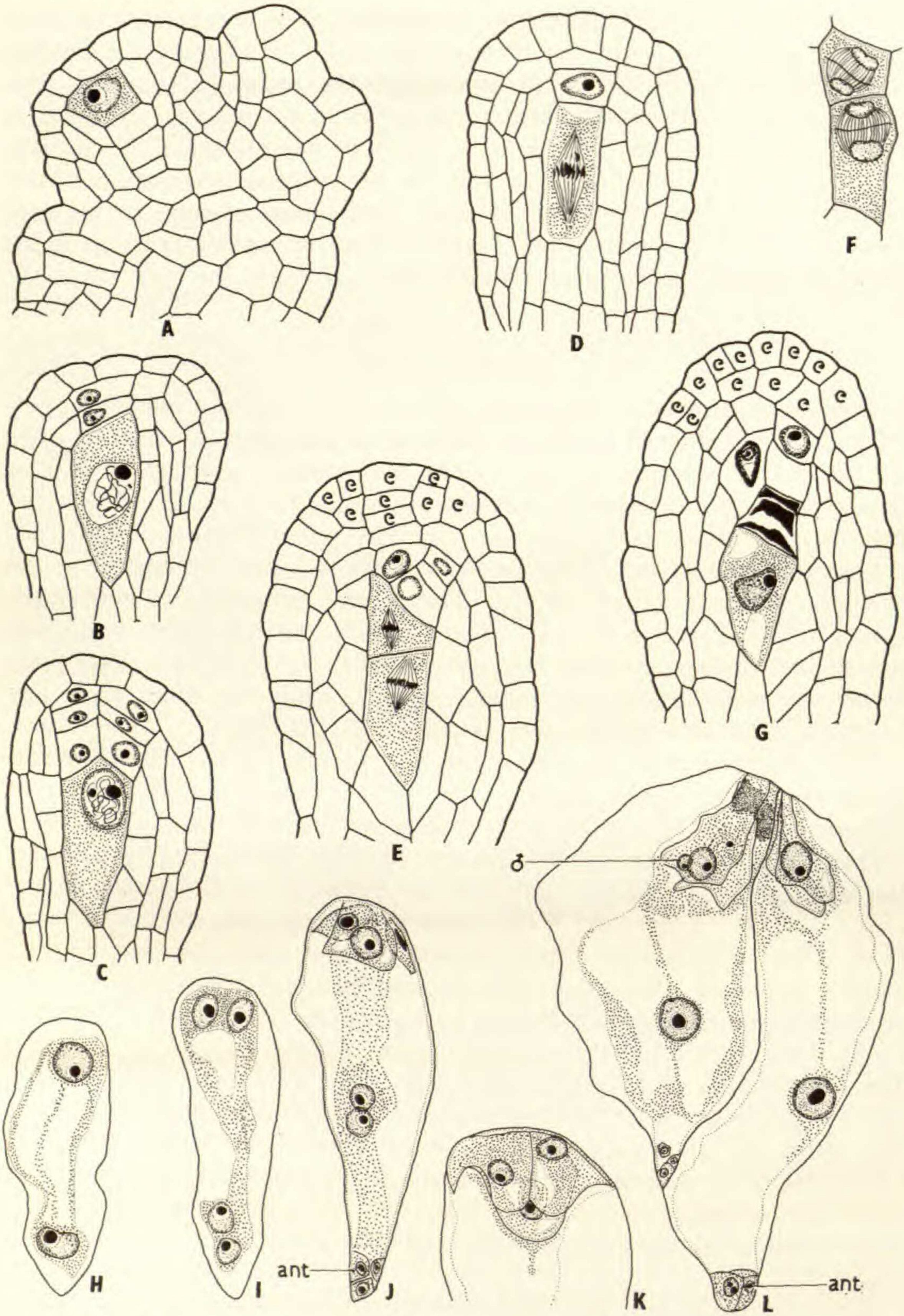

FIG. 3. *Drimys winteri*, megasporogenesis and female gametophyte (ant, antipodals; e, epidermis; ♂, male nucleus). A, longisection of ovular primordium showing a single-celled archesporium and primordia of two integuments; B, longisection of nucellus showing megaspore mother cell and two parietal cells; C, *the same*, megaspore mother cell and a 3-layered parietal tissue formed by the parietal cell; D, *the same*, megaspore mother cell at metaphase; E, longisection of nucellus, two dyad cells at metaphase II, the parietal

E) an evanescent cell plate is sometimes formed at Telophase I (Fig. 2E). At the end of homotypic division (Figs. 2F–J) simultaneous quadripartitioning occurs by furrowing. The microspores remain in permanent tetrads which may be tetrahedral or decussate (Figs. 2Q, U, V). At the beginning of gametogenesis, the nucleus of the microspore moves towards the proximal pole of the tetrad where it divides (Figs. 2R–T). The four microspores in a tetrad may show different stages in the formation of the generative cell (Fig. 2U). The wall between the two cells degenerates so that the generative cell, surrounded by a hyaline cytoplasmic sheath, comes to lie free within the cytoplasm of the vegetative cell (Fig. 2Z).

The pollen grains are monoporate and the pore is developed towards the distal end. The intine protrudes through the pore and shows maximum thickening in this region (Figs. 2Q–Z). As stated by Bailey and Nast (1943a) for *Drimys* section Wintera, here also a collar is present at the base of protruding intine (Figs. 2W, X). The pollen grains are shed in tetrads at the 2-celled stage (Fig. 2Z).

Megasporangium, Megasporogenesis and Female Gametophyte. The young carpel resembles a conduplicately folded leaf. The two approximated margins of the carpel are firmly concrescent except at the stigmatic region where the epidermal cells interlock. There are 15 or 16 anatropous, bitegmic and crassinucellate ovules. A single hypodermal archesporial cell differentiates in the nucellus (Fig. 3A) and divides transversely to form a primary sporogenous cell and a parietal cell. The latter undergoes repeated periclinal and anticlinal divisions to form a 2- or 3-layered parietal tissue (Figs. 3B–E). Meiosis I in the megaspore mother cell (Figs. 3C, D) results in a dyad, of which the micropylar cell is smaller (Figs. 3E, F). Both of the dyad cells divide simultaneously to form a linear or a T-shaped tetrad (Figs. 3E, F). The chalazal megaspore functions and the other three megaspores degenerate (Fig. 3G). Three successive mitoses result in a 2- (Fig. 3H) 4- (Fig. 3I) and 8-nucleate embryo sac (Figs. 3J–L). Thus, the development conforms to the Polygonum type. Occasional instances of twin embryo sacs were also observed (Fig. 3L).

Fertilization and Endosperm. Syngamy and triple fusion have been observed (Fig. 4A). The pollen tube is sometimes persistent during early stages of the endosperm development. The endosperm is *ab initio* cellular. The primary endosperm nucleus migrates towards the center of the embryo sac before its division (Figs. 4B, C) which is followed by the formation of a transverse wall (Fig. 4D). The next division in the two unequal cham-

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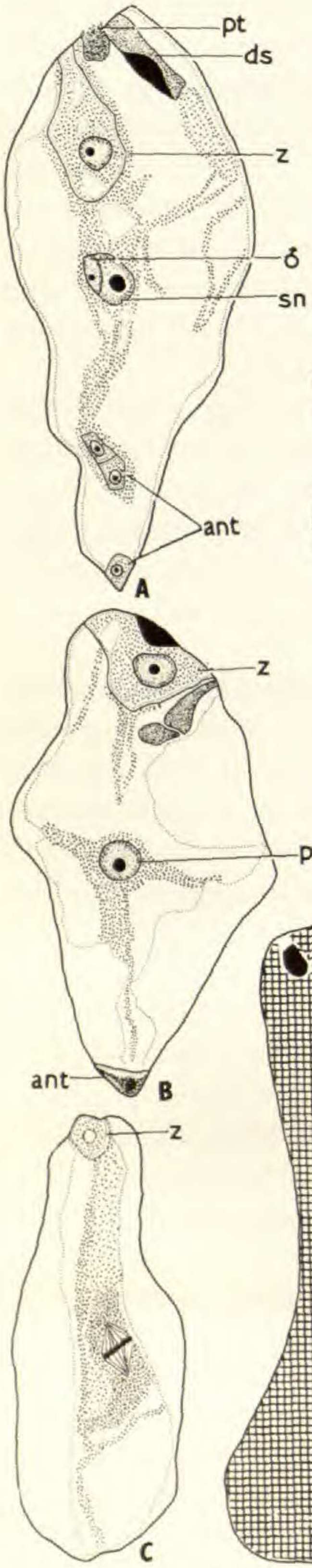
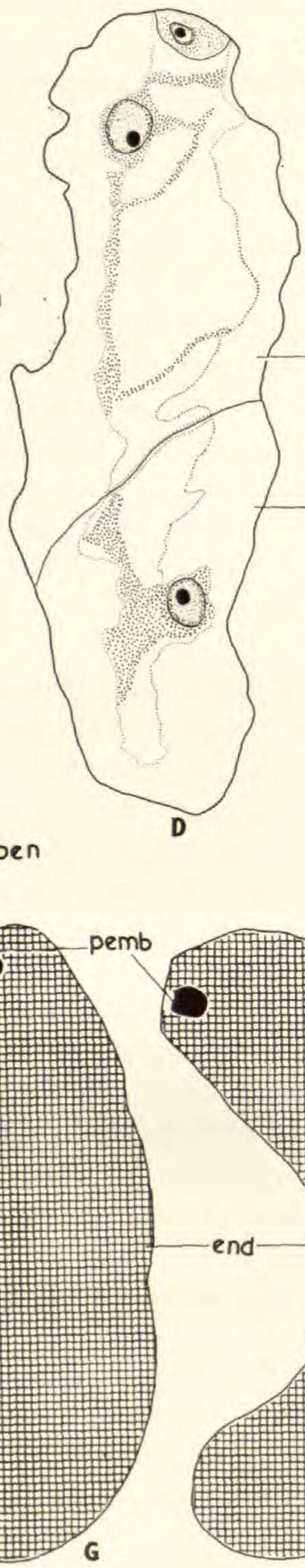
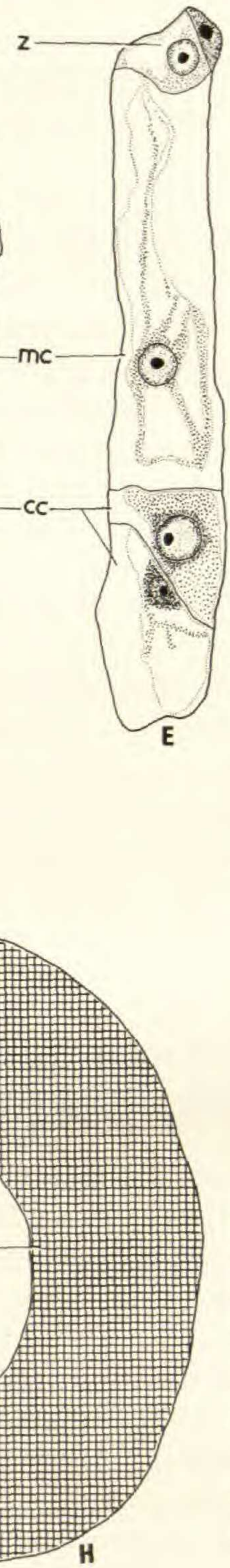
tissue is being contributed by both the parietal layer and the nucellar epidermis; F, two dyad cells showing telophase spindles indicating the formation of a T-shaped tetrad; G, longisection of nucellus showing tetrad with the chalazal functional and the other three degenerated megaspores; H, I, two- and four-nucleate embryo sacs; J, organized 8-nucleate embryo sac showing egg apparatus, two polar nuclei and three uninucleate antipodal cells; K, micropylar end of an embryo sac enlarged to show egg apparatus with hooked synergids; L, twin embryo sacs. A–E, and G, all × 465; F, H–L, all × 610.







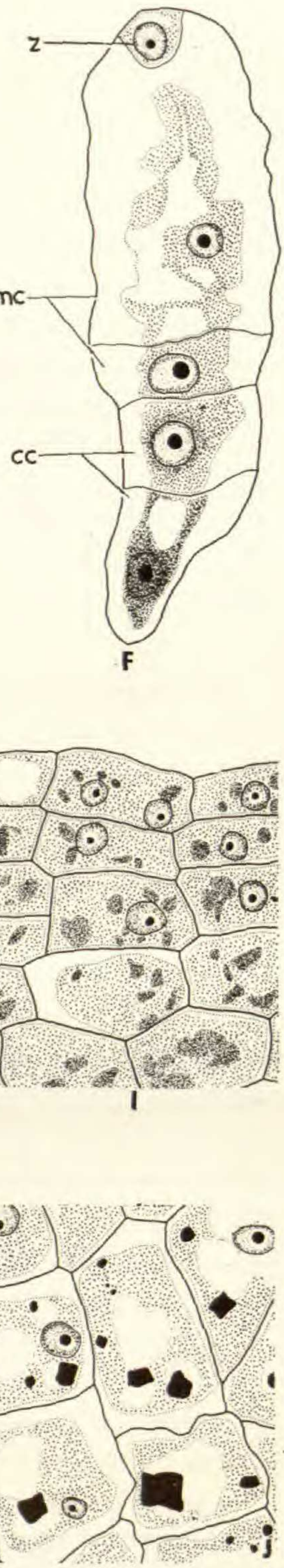


FIG. 4. *Drimys winteri*, endosperm (ant, antipodal cells; cc, chalazal chamber; ds, degenerated synergid; end, endosperm; ♂, male nucleus; mc, micropylar chamber; pemb, proembryo; pen, primary endosperm nucleus; pt, pollen tube; sn, secondary nucleus; z, zygote). A, embryo sac showing triple fusion, note the persistent remnants of pollen tube; B, *the same*, showing primary endosperm nucleus, zygote, remnants of degenerated synergids and antipodal cells; C, embryo sac with the primary endosperm nucleus in division; D–F, two-, three-, and four-celled endosperm stages, the chalazal chamber has divided into two cells of which the lower cell is degenerating; G, H, longisections of mas-

bers is transverse but the division in the chalazal chamber precedes that of the micropylar (FIG. 4E). The two cells formed in the micropylar chamber are again unequal, the smaller cell being towards the chalazal end (FIG. 4F). It appears that the chalazal chamber does not contribute much to the formation of the endosperm proper.

The endosperm soon becomes massive and at the 10-celled stage of the embryo it is made up of cells having prominent nuclei and dense cytoplasm. Later, the endosperm cells become packed with small round or oval brownish particles of unknown nature which did not give any positive test for starch, oil or proteins (FIGS. 4G, I). In mature endosperm the cells are large with little cytoplasm but are packed with bodies which stain darkly with hematoxylin (FIGS. 4H, J).

Embryogeny. The earlier stages observed were a zygote (FIG. 5A) and a nearly 20-celled proembryo which is rather irregularly organized (FIG. 5B). Perhaps the divisions do not correspond to any of the known types of embryogeny. From the globular stage onwards the embryo development is regular (FIGS. 5C–G) with a prominent suspensor and well demarcated protoderm. During late embryogeny periclinal divisions in the 6th or 7th subprotodermal layer begin the demarcation of the embryonal pith, procambium, and cortex in a globular proembryo (FIGS. 5H, I). The suspensor cells are filled with starch grains. In the oldest seed that we examined the embryo was at a pre-heart-shaped stage (FIGS. 5H–I). No more details could be obtained due to paucity of material.

Seed coat. At the megaspore mother cell stage the outer and inner integuments are 3-layered for the greater part of their length (FIG. 6A). During megasporogenesis brownish substances accumulate in some cells of both the integuments. Just after fertilization the cells of the outer integument and those of the inner epidermis of the inner integument at the micropylar region become packed with substances which stain dark red with safranin. Subsequently, the space between the outer and the inner integument becomes almost obliterated (FIG. 6B).

In a mature seed the testa is formed by the outer integument. The cells of the outer epidermis elongate radially, become thick walled, extremely hard, and packed with brownish contents (FIGS. 6C–E). Next to this are two layers of cells filled with tannin and the inner epidermis, which remains thin-walled with small nuclei and large vacuoles (FIG. 6C). The inner integument becomes almost crushed and is represented by one or two layers of compressed thin-walled parenchymatous cells.

An interesting feature is that in the mature seed the outer surface of

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sive endosperm at globular and post-globular stages of the embryo, respectively; I, part I in G enlarged to show a few cells of the endosperm which are densely cytoplasmic with prominent nuclei and filled with oval or globular particles; J, portion J in H enlarged to show a few endosperm cells, the cells are highly vacuolate and contain dark squarish particles of reserve food materials. A–C, × 550; D–F, × 440; G, H, × 30; I, J, × 360.

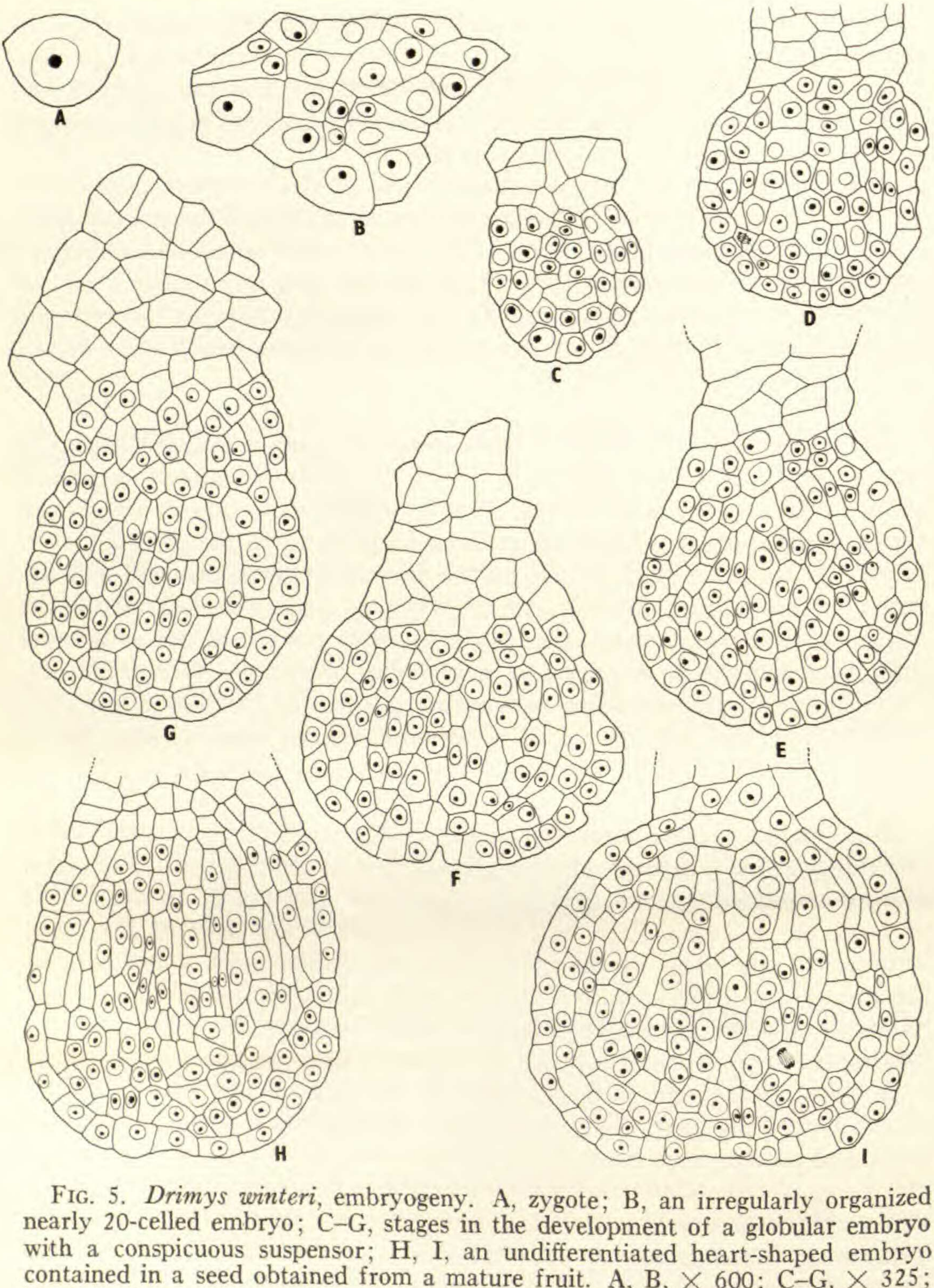

FIG. 5. *Drimys winteri*, embryogeny. A, zygote; B, an irregularly organized nearly 20-celled embryo; C–G, stages in the development of a globular embryo with a conspicuous suspensor; H, I, an undifferentiated heart-shaped embryo contained in a seed obtained from a mature fruit. A, B, × 600; C–G, × 325; H, I, × 265.

the seed coat is thrown into three or four ridges. The endosperm, however, is not ruminate (FIGS. 6D, E).

Pericarp. At the megaspore mother cell stage the ovary wall consists of ten to twelve layers of parenchymatous cells (FIG. 6F). Two or three

inner and outer layers are filled with brownish phenolic compounds. Numerous ethereal oil cells having a vacuolated cytoplasm and prominent nuclei are interspersed within the pericarp (FIG. 6F). During post-fertilization stages the wall becomes 20- to 25-layered. The number of ethereal oil cells and tannin cells also increases (FIG. 6G). When the embryo is at the globular or post-globular stage the pericarp becomes nearly 30-layered and the outer and inner epidermis are greatly flattened. The number of tannin cells increases and they become completely filled with such substances. The parenchymatous cells become greatly stretched and break down (FIG. 6H). No meristematic activity of the pericarp as has been observed in *Pseudowintera* (Bhandari, 1963) is seen here.

DISCUSSION

Embryological observations on the Winteraceae are rather meager and are confined to *Drimys*, *Pseudowintera*, and *Zygogynum*. These are discussed in the light of the present work on *Drimys winteri*.

The anther tapetum is glandular in *Pseudowintera axillaris* (Sampson, 1963) and *Zygogynum* (Swamy, 1952) and amoeboid in *P. colorata* (Bhandari, 1963). Bhagavathi Kutti Amma's (1938) report of amoeboid tapetum in *Drimys* is doubtful since the present investigation has clearly established its glandular nature. In *Zygogynum* the nuclei in the tapetal cells divide and fuse to become polyploid but in *Pseudowintera* they remain binucleate. In *Drimys*, however, the tapetum becomes irregularly bi-layered with binucleate cells which often become polyploid.

In *Zygogynum baillonii* (Swamy, 1952) a centripetal furrow is formed after Meiosis I. Rarely an incipient equatorial cell-plate is also laid down at the end of heterotypic division but quadripartitioning of the microspores is completed only after homotypic division. Contrary to this, in *Pseudowintera colorata* (Bhandari, 1963) the division is simultaneous without any evanescent cell-plate while in *P. axillaris* (Sampson, 1963) and *Drimys* (present investigations) it is formed after Telophase I. The phylogenetic implication of the presence of such an evanescent cell-plate in these and some other primitive genera (*Magnolia*, cf. Farr, 1918) is not clear, although it might perhaps represent the relics of an ancestral feature. The pollen grains are monoporate and are shed at the 2-celled stage. The generative cell is cut off towards the proximal end. In *Zygogynum* (Swamy, 1952) and *Pseudowintera colorata* (Bhandari, 1963) the divisions of the microspore nucleus in a tetrad are simultaneous. In *Pseudowintera axillaris* (Sampson, 1963) and *Drimys winteri* (present report) the microspores in the same tetrad show different stages of division.

The embryo sac is of the Polygonum type in all three genera. The synergids and antipodal cells degenerate soon after fertilization in *Zygogynum* (Swamy, 1952) but in *Pseudowintera colorata* (Bhandari, 1963) and *Drimys winteri* (present work) they persist for a few divisions of the endosperm. A twin embryo sac has been observed in *D. winteri* (present work).

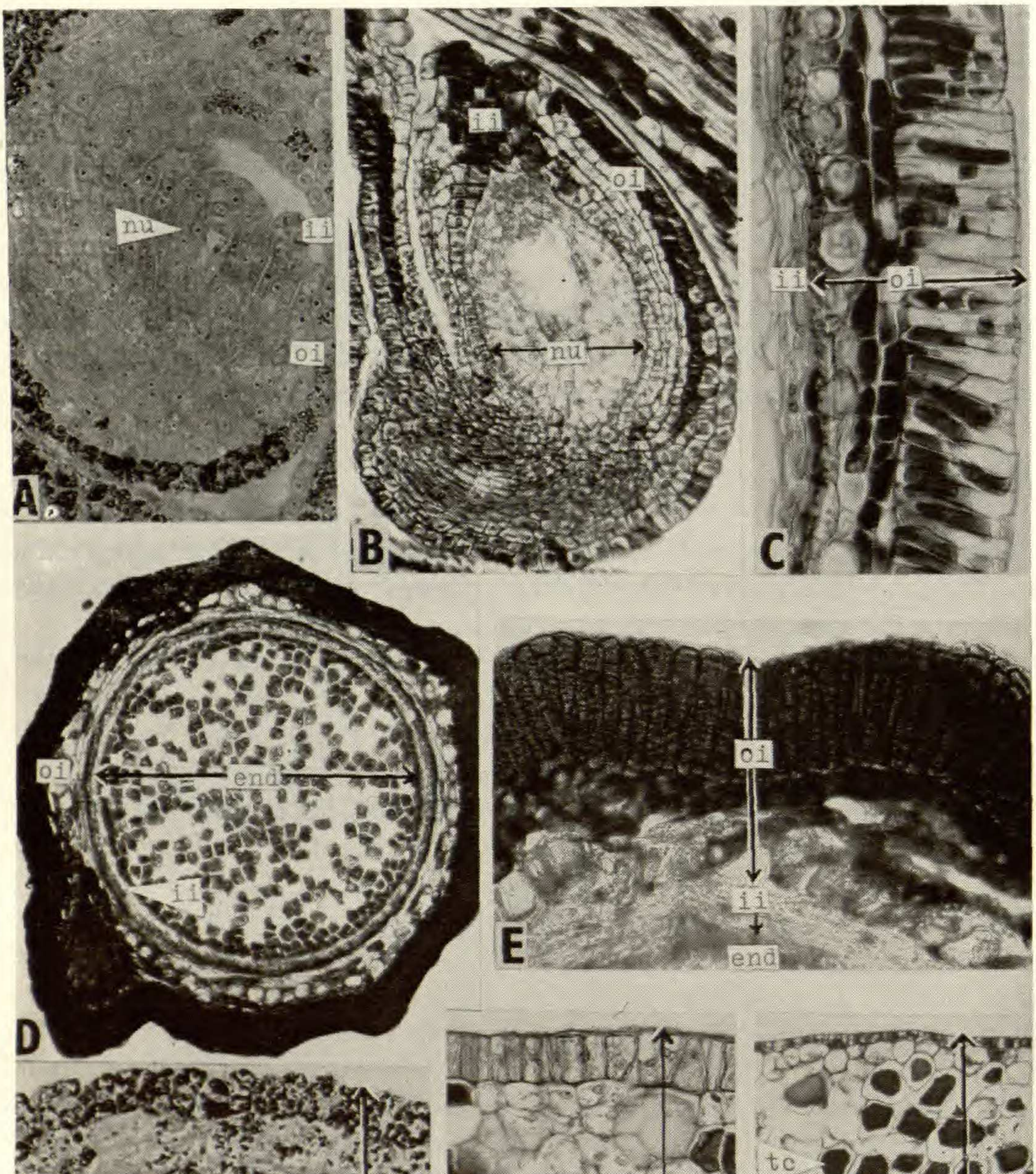

FIG. 6. *Drimys winteri*, seed coat and pericarp (ec, ethereal oil cells; end, endosperm; ii, inner integument; ie, inner epidermis; nu, nucellus; oi, outer integument; per, pericarp; tc, tannin cells). A, longisection of ovule at mega-

Triple fusion precedes syngamy in *Pseudowintera colorata* (Bhandari, 1963) and *Drimys winteri* (present work). In *Zygogynum baillonii* (Swamy, 1952), *P. colorata* (Bhandari, 1963) and *Drimys winteri* (present work) the endosperm is cellular. The division of the primary endosperm nucleus is invariably transverse in *Zygogynum* (Swamy, 1952), but may be transverse or longitudinal in *P. colorata* (Bhandari, 1963). In *D. winteri*, Strasburger (1905) reported nuclear endosperm. A reinvestigation (present observations) of this species, however, has shown this to be erroneous. The endosperm, therefore, is *ab initio* cellular in all the genera so far investigated.

The present investigation is the only record of embryogeny indicating that the earlier divisions of the developing embryo are irregular. However, from the globular stage onwards the development is regular. In *Pseudowintera colorata* (Bhandari, 1963) the embryo is dicotyledonous but in *Drimys winteri* it remains undifferentiated.

In *Pseudowintera colorata* (Bhandari, 1963) and *Drimys* (present work) the seed coat is formed by elongated tannin-filled cells of the outer epidermis, along with two or three hypodermal layers of thick-walled cells of the outer integument. In *Drimys*, however, (present work) the outer epidermis of the outer integument is variously ridged.

The pericarp is composed of 20 to 25 layers of parenchymatous cells with interspersed ethereal oil cells in both *Pseudowintera colorata* (Bhandari, 1963) and *Drimys* (present work). In *P. colorata* the unilocular ovary becomes chambered during the maturation of fruit because of meristematic activity of pericarp between the ovules. No such meristematic activity has been observed in any other winteraceous member.

Systematic position. Bentham and Hooker (1862–67) included *Drimys* together with *Illicium* in the tribe Wintereae of the Magnoliaceae.

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spore mother cell stage to show the two integuments which are 3- or 4-layered; B, *same* at the zygote stage, the outer integument is 4-layered at the tip and 5-layered below with outermost 2 layers completely filled with tannin, inner is 5- or 6-layered only in the micropylar region, these cells are packed with tannin; C, a magnified part of the seed coat at the preglobular stage of the embryo, the outer integument has elongated cells completely filled with tannin, the innermost layer consists of large parenchymatous cells, the inner integument persists as a thin layer of compressed parenchymatous cells; D, transection of mature seed to show the ridges on the hard seed coat (hand section); these ridges are restricted only to the outer epidermis of the outer integument; E, a part of D magnified to show the details of the seed coat; F, transection of a carpel at the megaspore mother cell stage of the ovule showing the 10 to 12 parenchymatous layers of the pericarp, the outer and the inner two or three layers are filled with tannin; a few ethereal oil cells are also seen; G, a magnified part of transection of post-fertilized carpel, the pericarp is 15 or 16 layers thick, the epidermal cells are radially elongated and prominent, a number of tannin cells and ethereal oil cells are interspersed in the rest of the parenchymatous tissue; H, *same* at the globular stage of embryo, the outer and the inner epidermal layers are compressed, between these are 20 to 25 layers of parenchymatous cells with numerous tannin cells and empty ethereal oil cells. A, × 225; B, × 100; C, × 110; D, × 100; E, × 200; F, × 435; G, × 140; H, × 35.

Van Tieghem (1900) grouped all the members with vesselless xylem under Homoxylées. He placed five winteraceous genera (*Drimys*, *Bubbia, Belliolum*, *Exospermum* and *Zygogynum*) in this group whereas Dandy (1933) later added the sixth genus, *Pseudowintera*, from New Zealand. Barkley (1966) has recognized three more genera, namely, *Tetrathalamus*, *Wintera*, and *Lassonia* in this family but includes *Belliolum* with *Drimys*. Hutchinson (1959), too, considers *Tetrathalamus* a distinct genus of the Winteraceae although Smith (1943) merges this genus with *Bubbia* as *B. montana*. Embryological information on *Tetrathalamus*, *Lassonia* (=*Magnolia*, see Willis, 1966) and *Wintera* is wanting and any consideration regarding their taxonomic position must await such data.

Hutchinson (1959) also believes that *Degeneria* is related to *Exospermum* and *Zygogynum* and should, therefore, be included in the Winteraceae. Bhandari (1963) has compared the embryological features of the Winteraceae and *Degeneria* and supported the conclusions of Bailey and Smith (1942) that *Degeneria* be assigned to a separate family, the Degeneriaceae. However, no light has yet been thrown, embryologically, on the relationship of Winteraceae with the Illiciaceae. The morphological and embryological characters of these families are compared in the following table:

Table 1

	WINTERACEAE	ILLICIACEAE
HABIT	Trees and shrubs.	Shrubs and trees.
*WOOD ANATOMY	Vesselless, heterogeneous ray structure. Tracheary pitting scalariform.	Vessels present, multiseriate ray structure. Tracheary pitting scalariform to opposite.
*NODAL ANATOMY	Trilacunar.	Unilacunar, single-traced
FLOWERS	Actinomorphic to zygomorphic, bisexual or unisexual, hypogynous.	Actinomorphic, bisexual, hypogynous.
*CALYX	Calyptrate; sepals bract-like, connate.	No differentiation into calyx and corolla; tepals numerous.
*COROLLA	Petaloid to scale-like, reduction from many to 2.	
*ANTHER	Microsporangia subterminal, or lateral, protuberant or embedded.	Microsporangia lateral, protuberant.
*ENDOTHECIUM	Endothecium extends towards the connective region.	Endothecium does not extend towards connective region.

* Points of difference.

Table 1. (*Continued*)

*Tapetum	Amoeboid or secretory, cells binucleate, parietal in origin.	Glandular, irregularly 2-layered, cells binucleate, originates from sporogenous tissue.
Tetrads	Tetrahedral, tetragonal, or decussate.	Tetrahedral.
*Pollen grains	In permanent tetrads, monoporate, generative cell cut off at proximal end, intine comes out of the germ pore.	Individual, tricolpate, isopolar.
*Carpel	Open or closed, conduplicate, sessile or stipitate.	Closed, sessile.
Ovule	Anatropous, bitegmic, crassinucellate.	Anatropous, bitegmic, crassinucellate.
Female gametophyte	Polygonum type, antipodals degenerate after fertilization.	Polygonum type, antipodals ephemeral.
Endosperm	Cellular.	Cellular or nuclear?
*Embryogeny	Irregular.	Asterad type.

* Points of difference.

It is clear from the above Table that *Illicium* differs from *Drimys* and allied genera in numerous embryological and morphological features which negate its relationship with the Winteraceae and support its inclusion in a separate family, the Illiciaceae (cf. Eames, 1961; Hayashi, 1960, 1963; Kapil & Bhandari, 1964; Smith, 1947). However, at the same time it has certain features which indicate its ranalian affinities.

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